ACTOSTROMA GEN. NOV., A JURASSIC STROMATOPOROID FROM MAKTESH HATHIRA, ISRAEL

by R. G. S. HUDSON

ABSTRACT. Stromatoporoids from the Coral-stromatoporoid beds (Upper Jurassic: Argovian–Rauracian) exposed in the Kurnub Anticline of Maktesh Hathira, southern Israel, are shown to be characterized by lateral astrotubes and considered to be transitional to the Hydroidea. They are described as *Actostroma damesini*, *A. nasri*, and *A. kühni*, gen. et spp. nov.

INTRODUCTION

THE Jurassic succession (Callovian to Tithonian) exposed in the Kurnub Anticline at Wadi Hathira, about 35 kilometres south-east of Beersheba, northern Negev, southern Israel, includes, near the top of the succession, 58 metres of limestone and marl with abundant corals and stromatoporoids. The fauna is of Rauracian facies and of Upper Argovian (Rauracian) age. The stromatoporoids include various species of *Promillepora*, *Shuqraia*, *Steinerina*, and *Stromatoporina*, *Shuqraia* being by far the most common. *Promillepora kurnubi* Hudson, *P. pervinquieri* Dehorne, *P. douvillei* (Dehorne) and *Steinerina somaliensis* (Zuff.-Com.) were described from these beds (Hudson 1956). A generalized account of the Jurassic succession is given by Blake (1936), Shaw (1947), Ball and Ball (1953), and Wiener (1955). The specimens described in this paper were collected by the author. Registration numbers preceded by the Letter H are those of specimens in the collection of the Department of Palaeontology, British Museum (Natural History), London.

The author here records his thanks to those geologists of the Iraq Petroleum Company whose work made this paper possible and in particular to F. E. Wellings, Chief Geologist, who first investigated the area and to L. Damesin who, with S. Nasr, mapped the area and introduced the author to it. Permission to publish this paper has been generously given by the Directors and Chief Geologist of the Iraq Petroleum Company.

STROMATOPOROID SKELETAL MORPHOLOGY

Methods of investigation. The internal structure of the stromatoporoids described in this paper was first investigated by the examination of tangential and radial thin-sections. Examination by transmitted light of the tangential sections failed to distinguish between shallow structures such as coenosteal tubules and those, such as the astrotubes, that have depth, a defect only partly remedied by the examination of the thin sections by reflected light (Pl. 16, figs. 4–6). The two types of structures are, however, very distinct on polished surfaces where the deeper structures are darker in colour (Pl. 16, figs. 8–14). Internal structure was, therefore, mainly investigated by the examination of serial polished surfaces.

The measurements of pillars, lamellae, coenosteal tubules, &c., recorded in the follow-

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ing descriptions of the various species are very approximate. They indicate the commonly occurring dimensions and not the average, or the range.

Lamellae. The skeletal elements of the Palaeozoic Stromatoporoidea consist, in the main, of vertical pillars or vertical lamellae, and transverse laminae. In many genera these are histologically different and thus there is justification for the distinction inferred by the use of the terms lamellae and laminae. In the Mesozoic Stromatoporoidea vertical and horizontal elements have a similar structure and origin, and are therefore both denoted lamellae and distinguished as vertical lamellae and transverse lamellae.

Latilamellae. These are the concentric zones of the reticulum, alternately the one lighter in colour than the other (Pl. 16, figs. 7–14), a colour difference occurring in both the skeletal elements and the spaces between them. The difference is partly due to an actual difference in the colour of the skeletal elements, due to a variation in texture of the skeletal tissue, and partly due to the greater thickness of pillars and transverse lamellae in the lighter coloured (compact-textured) zone. This reduces the size of the spaces between the skeletal elements and so, having less depth, they are, by reflected light, lighter in colour. There are also occasional thinner bands in which the transverse lamellae are more or less as equally developed as the vertical lamellae, thus giving a marked reticulation in radial section (Pl. 16, figs. 11, 14). They may include transverse lamellae of considerable continuity.

Skeletal tissue. The tissue of the pillars and lamellae of the Mesozoic stromatoporoids is essentially trabecular formed by radial or bilateral secretion, normally crystalline and fibrous, continuing from retreating areas of calcification and forming, in the case of a pillar, calcite fibres radial to an axial strand of superposed 'centres of calcification' or trabecular centres. In the case of a lamella such strands laterally coalesce to form a median band of trabecular centres. Such trabecular strands or median bands are finely granular and are usually darker than their sheath of fibres. They may be simple, that is, formed of superposed single centres, or composite, formed of superposed groups of centres. Such groups may be loose or compact, and may form the entire trabecula. The angular relationship of the fibres to the axial strand or median band varies. They may be, as in *Actinostromaria*, perpendicular, radially in the pillar, bilaterally in the lamellae. Such skeletal tissue is here termed *orthogonal.* They may diverge upwards, again radially or bilaterally, as in *Stromatoporina*, a form of divergence often termed as 'fasciculate upwards' or 'fountain-like (*jet d'eau*)'. Such skeletal tissue is here termed *clinogonal.* When the trabecular strands or bands are composite, the angle of divergence of the fibres varies, though more generally outwards than upwards. The fibres may be generally perpendicular to the axis or diverge slightly upwards, though rarely clearly defined or constant: when the centres are isolated the fibres may approximate to sphaerical radial. Such tissue is here termed *heterogonal.*

It is doubtful if the tissue of *Burgundia* could be called trabecular. It is due to unilateral secretion of fibres perpendicular to a plane of calcification centres. Such tissue is termed *unilateral orthogonal.*

Astrorhizae and astrorhizal systems. In its simplest form, the stromatoporoid astrorhizal system consists of a number of shallow, radiating furrows or gutters on the surface of the coenosteum, without walls, branching distally, and passing distally without a marked break into the reticulum; they may join at the centre or there may be, at the centre, one or more shallow depression or pits. It is these furrows which were originally called astrorhizae and it is with that meaning the term is used in this paper. The astrorhizae may, or may not, be incorporated into the coenosteum by subsequent growth of the reticulum. When they are they form astrorhizal lateral tubes, horizontal or oblique, according as to whether the surface on which they formed was level or axially raised.

Astrotubes. In many Mesozoic stromatoporoids the axial part of the astrorhizal system consists of one or more closely grouped vertical tubes, wider than the coenosteal tubules and usually tabulate. These vertical tubes are here called axial astrotubes. In *Stromatoporellina*, *Milleporella*, and such forms as '*Stromatopora*' *choffati* Dehorne, the wide tabulate astrorhizae are divided into chambers of varying length, some, especially near the axis, being almost circular. They continue in depth so that in vertical section they are variously exposed as tabulate vertical tubes: cut obliquely, as they often are in vertical sections, they appear as tabulate lateral chambers. In *Steinerella* the process of isolation of these chambers is carried still farther and, distally, the astrorhizal radii may include of a number of tabulate vertical tubes, adjacent or separate, though clearly aligned. In the species of *Actostroma* described in this paper, there are, variously distributed within the coenosteum, a number of such vertical tubes. They are, more or less, linearly arranged about an axis, the lines of tubes branching distally in a pattern comparable to that of the astrorhizae of the more simple systems. It is suggested that all such vertical tubes, whether occurring along astrorhizae or aligned in a comparable pattern, should be termed lateral astrotubes.

Lateral astrotubes originate from coenosteal tubules in astrorhizae or along the astrorhizal radii. Their abundance, the pattern they form, and their direction of upward growth varies with the species. They are independent of the latilamellae. When, as in *Actostroma*, they do not occur in astrorhizae, their relationship to the astrorhizal system is shown not only by their alignment but sometimes by the specialization, to a variable degree, of the coenosteal tubules separating them along the radii. In *Actostroma nasri*, for instance, such tubules are elongated in the direction of the radii and are thus aligned. They are also generally slightly larger than those in the main reticulum. This difference continues in depth so that in vertical sections, the astrorhizal radii, apart from the lateral astrotubes, are marked by coenosteal tubules which are continuous, slightly wider and more regularly reticulate than the remainder (Pl. 16, fig. 14). When such a link does not exist and the astrotubes are only vaguely aligned, as in *Actostroma damesini*, they approach the autotubes of the Milleporidiidae which have no alignment. The two structures are analogous.

Astrorhizal symmetry. In *Actostroma nasri* and *A. kühni* there are six main astrorhizal radii (see Pl. 16, figs. 7, 9, 13), usually in two groups of three. This sixfold symmetry also occurs in *Actostromaria stellata* Haug (see Steiner 1932, p. 38). Though the pattern is confused by early bifurcation, the figures (Steiner 1932, pl. 3) of *Actinostromaria lugeoni* Steiner also suggest sixfold astrorhizal symmetry. These and other examples suggest that a sixfold astrorhizal symmetry is characteristic of the Actinostromariidae. In other stromatoporoids the pattern of the astrorhizal radii is also sixfold and it may be that the basic astrorhizal symmetry of other groups is also hexameral.

SYSTEMATIC PALAEONTOLOGY

Classification. The Jurassic–Cretaceous hydrozoa which have been compared to the Palaeozoic Stromatoporoidea can be divided into two groups, those such as the Milleporidiidae, without astrorhizae or related structures, and those such as the Stromatoporinidae, Actinostromariidae, and Burgundiidae which have astrorhizae or related structures. The former group have been considered to belong to the Hydroidea (comprising, with others, all recent hydrozoa with a calcareous skeleton, including the Milleporina and the Stylasterina) and the latter to the Stromatoporoidea (Kühn 1928, 1939; Alloiteau 1952; Hudson 1956). Galloway and St. Jean (1956) and St. Jean (1957), however, consider that, on the basis of tissue structure, only Palaeozoic forms should be included in the Stromatoporoidea and that the Mesozoic forms should be allocated to the Sphaeractinoidea.

The author, however, considers that the occurrence in both Palaeozoic and Mesozoic forms of astrorhizal structures is the most important diagnostic feature of both groups, possibly the only one of phylogenetic significance and, as such, it justifies the inclusion in the Stromatoporoidea of those Mesozoic forms in which it occurs. Nevertheless, the difference in the microstructure of the skeletal tissue of Palaeozoic and Jurassic–Cretaceous forms is, in the opinion of the author, a fundamental one and, by and large, excludes the Jurassic–Cretaceous stromatoporoids from the families into which the Palaeozoic forms are grouped. The thesis that various groups in the Stromatoporoidea are ancestral to various groups in the Hydroidea is possibly a true one: it cannot, however, be demonstrated and should not, as yet, be taken into account in classification.

The various families of the Jurassic–Cretaceous Stromatoporoidea can be grouped according to the direction of growth of the fibres of the skeletal tissue and the grouping of the trabecular centres. There are those families, such as the Stromatoporinidae and Milleporellidae, in which the fibres are bilaterally clinogonal, those, such as the Actinostromariidae, in which they are bilaterally orthogonal or heterogonal, and those, such as the Burgundiidae, in which they are unilaterally orthogonal. It is not considered advisable to give these groups taxonomic rank until further work has been done on the structure of the skeletal tissue.

Order STROMATOPOROIDEA

Family ACTINOSTROMARIIDAE Hudson 1955

Diagnosis. Stromatoporoidea with orthogonal reticulum of vertical and transverse lamellae. Skeletal tissue orthogonal or heterogonal. Astrorhizal system of axial astrotubes and astrorhizae, or, of lateral astrotubes with, or without, astrorhizae.

Remarks. The above diagnosis is framed to include two groups of genera: one including the nominate genus *Actinostromaria* Haug 1909 (type species *A. stellata* Haug 1909) and the allied genus *Actinostromarianina* Lecompte 1952 (type species *A. dehorneae* Lecompte 1952); the other including the genera *Stromatorhiza* Bakalow 1906 and *Actostroma* gen. nov. All the above have an orthogonal reticulum but differ in the structure of their skeletal tissue, which in the first group is bilaterally orthogonal, and in the second group is bilaterally heterogonal. The enlargement of the family diagnosis to include such different genera is justified by the great similarity of their reticulum and by the consideration that, in the opinion of the author, such heterogonal tissue is ancestral to orthogonal tissue. The above genera are divorced from the Actinostromatidae Nicholson 1886, in which some of them have been included, because of the difference of their fibrous skeletal tissue from the compact skeletal tissue of *Actinostroma* (Lecompte 1956, p. F127).

In a recent paper (Hudson 1957) *Stromatorhiza granulosa* (Koby) was redescribed, its characteristic structures shown to be an orthogonal reticulum, heterogonal skeletal tissue, astrorhizae, and astrotubes. The genus was placed in a new family, the Stromatorhizidae, characterized by heterogenal tissue and thus distinct from the Actinostromariidae then defined by definite orthogonal tissue only. The family Actinostromariidae as now redefined would include *Stromatorhiza*: the family Stromatorhizidae is therefore no longer required.

Genus ACTOSTROMA gen. nov.

Type species *Actostroma damesini* sp. nov.

Diagnosis. Actinostromariidae with nodular encrusting coenosteum and orthogonal latilamellate reticulum of dominant vertical pillars linked by discontinuous transverse bars or lamellae. Coenosteal surface even, with open-vermiculate or tubular ostea. Skeletal tissue heterogonal, of feebly developed fibres, irregularly perpendicular or slightly diverging upwards from a broad composite axial strand or median band of trabecular centres. Lateral astrotubes abundant. Astrorhizae present or absent. No lateral astrorhizal tubes. Tabulae virtually absent or present only in astrotubes.

Remarks. The distribution of the astrotubes and the complete lack of astrorhizae in *Actostroma damesini* is unique and justifies the founding of a new genus. But for the feeble radial alignment of the astrotubes which indicate an astrorhizal origin, the species could quite well have been considered as an hydroid and not a stromatoporoid. The widening of the genus to include *A. kühni* characterized by astrorhizae is perhaps not justifiable. The certain allocation of that species awaits the clarification of Germovšek's genera discussed below.

The hydrozoan fauna described by Germovšek (1954) from the Upper Jurassic (Tithonian) of Slovenia, Yugoslavia, includes stromatoporoids characterized by a nodular coenosteum, an orthogonal reticulum, and vertical tubes. These were all considered to be new species and, generically, variously allocated to *Actinostroma* Nicholson, *Actinostromaria* Haug, and the three new genera, *Actinostromina* Germovšek, *Astrostylopsis* Germovšek, and *Trupetostromaria* Germovšek.

Some of Germovšek's species have considerable resemblance to the species of *Actostroma* described in this paper and the question arises as to whether *Actostroma* is a synonym of one or other of Germovšek's genera. Unfortunately the illustrations of his species do not include those of tangential surfaces or thin-sections in which a pattern of astrotubes, the main diagnostic feature of *Actostroma*, could be seen nor are his descriptions adequate since there is lack of definition of the various structures to which he refers: 'astrorhizal branches', for instance, might be astrorhizae or lateral astrotubes. The only illustration, for instance, of *Actinostromaria tubulata* Germovšek is that of a radial section which might be that of a species of *Actostroma*.

The forms most like species of *Actostroma* are those allocated to his new genera *Astrostylopsis* and *Trupetostromaria*, both of which are erroneously allocated to a family Trupetostromidae Germovšek 1954 on a mistaken structural similarity to its designate genus *Trupetostroma* Parks 1936, a genus of Devonian age. Both *Astrostylopsis* and *Trupetostromaria* are, like *Actostroma*, characterized by a skeletal tissue which is more or less heterogonal and both, again like *Actostroma*, have abundant vertical tubes. Those in *Astrostylopsis* are sporadically distributed in the coenosteum (Germovšek 1954, pl. 7, fig. 1*b*) and are considered by Germovšek to be individual axial tubes. In *Trupetostromaria* they are extensively and fairly closely distributed in the coenosteum and are also considered by Germovšek to be individual axial tubes. In neither genera is there evidence of alignment of astrotubes, the diagnostic feature of *Actostroma* gen. nov. The equation of *Astrostylopsis* with *Stromatorhiza* Bakalow (Hudson 1957) is now considered premature.

In 1955 Yabe and Sugiyama founded a genus *Tosastroma* which they placed in the Milleporellidae and to which they allocated two species, *T. tokunagai* Y. and S. (by original designation the type species) and *T. kiiensis* Y. and S. The types of both species are from the Torinosu Limestone (Upper Jurassic) of Japan. The author is of the opinion that the two species are not cogeneric. *T. kiiensis* has an orthogonal reticulum of irregular vertical pillars and transverse bars, the former dominant, the latter very discontinuous, a pattern very much like that of *Actostroma damesini*. Within the reticulum there are bands in which the vertical pillars are coarser and closer, again very much like *A. damesini*, but differing from that species in that the transverse elements in these bands are tabulae. Scattered in the reticulum but not mentioned by Yabe and Sugiyama, are wider unwalled tubes which might quite well be astrotubes, though they have no alignment. No indication is given of the tissue structure. In the opinion of the author *T. kiiensis* should be placed in the Actinostromariidae. Its bands of tabulate reticulum exclude it from *Actostroma*. It is evidently a closely allied form possibly demanding a new genus.

It is possible that *Actinostroma presalevensis* Zuff.-Com. and *Actinostromaria darroensis* Zuff.-Com. from the 'Oolitico medio' (Lusitanian) of Italian Somaliland and Ethiopia (Zuffardi-Comerci 1932; Wells 1943) are species of *Actostroma*. It has not, however, been possible to locate the type specimens of these species and since the description and figures are inadequate, generic determination has not been possible.

Actostroma damesini sp. nov.

Plate 15, figs. 1, 4; Plate 16, figs. 3, 5, 8, 10; Plate 17, figs. 3–5, 9; text-figs. 1–3

Type specimens. Holotype: H 4890, two pieces and thin-sections *a*, *b* (Pl. 15, fig. 1; Pl. 16, figs. 3, 5, 8, 10; Pl. 17, fig. 9; text-fig. 3). Paratypes: H 4888, one piece and thin-sections

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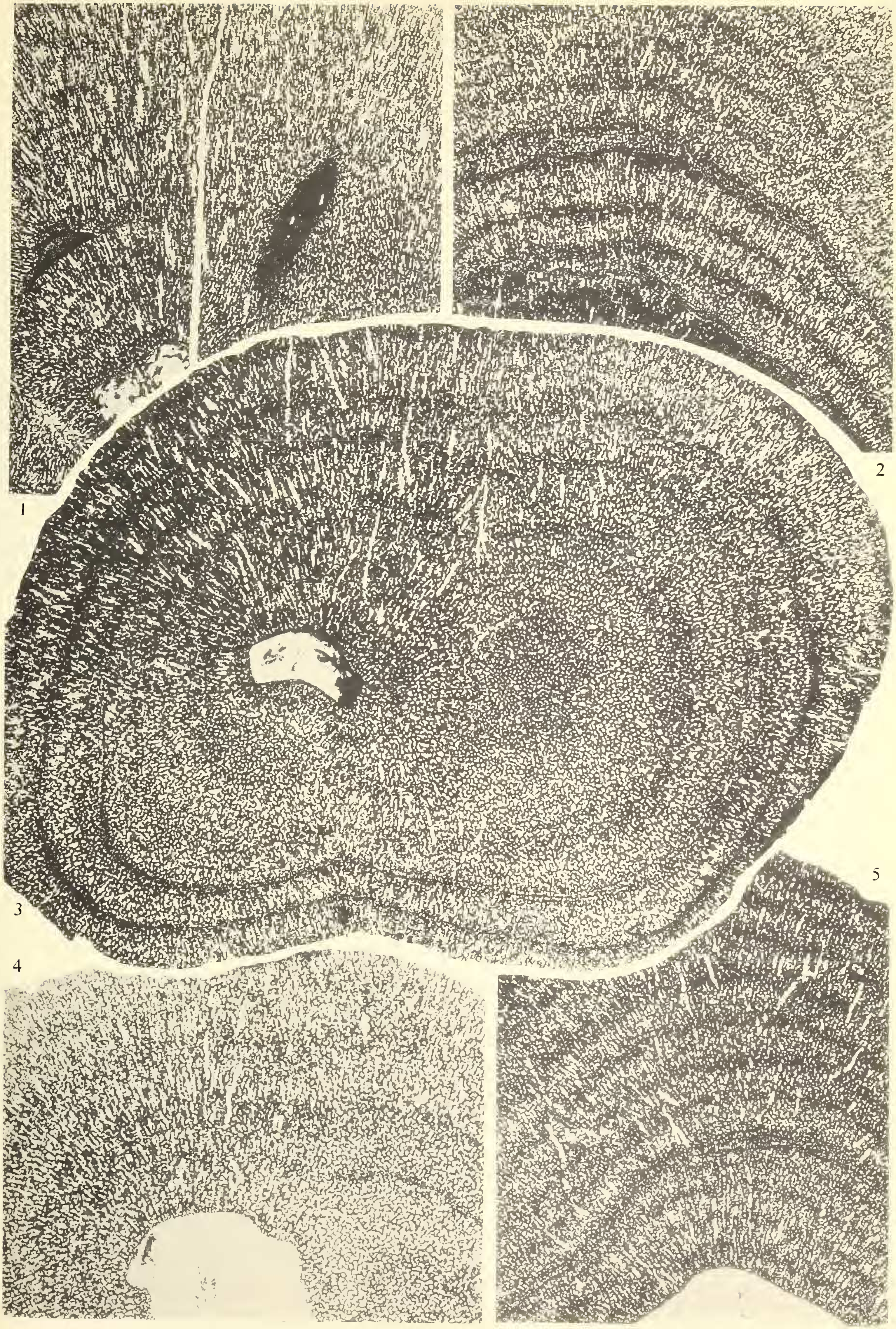
EXPLANATION OF PLATE 15

Thin-sections, photographed by transmitted light and untouched, of specimens from Coral-stromatoporoid beds, Kurnub Limestone (Upper Jurassic), Maktesh Hathira, Israel. The darker bands are the compact latilamellae (light-coloured in reflected light) in which the skeletal elements tend to be lamellae rather than pillars. On this plate the fine mesh of these bands is not always shown so that the band appears more compact and darker than it actually is.

Figs. 1 and 4. *Actostroma damesini* sp. nov. 1, radial section, H 4890a, ×4·1, from holotype, showing unwalled lateral astrotubes. 4, oblique and, lower right, tangential section, H 4889b, ×5·2, showing initial reticulum.

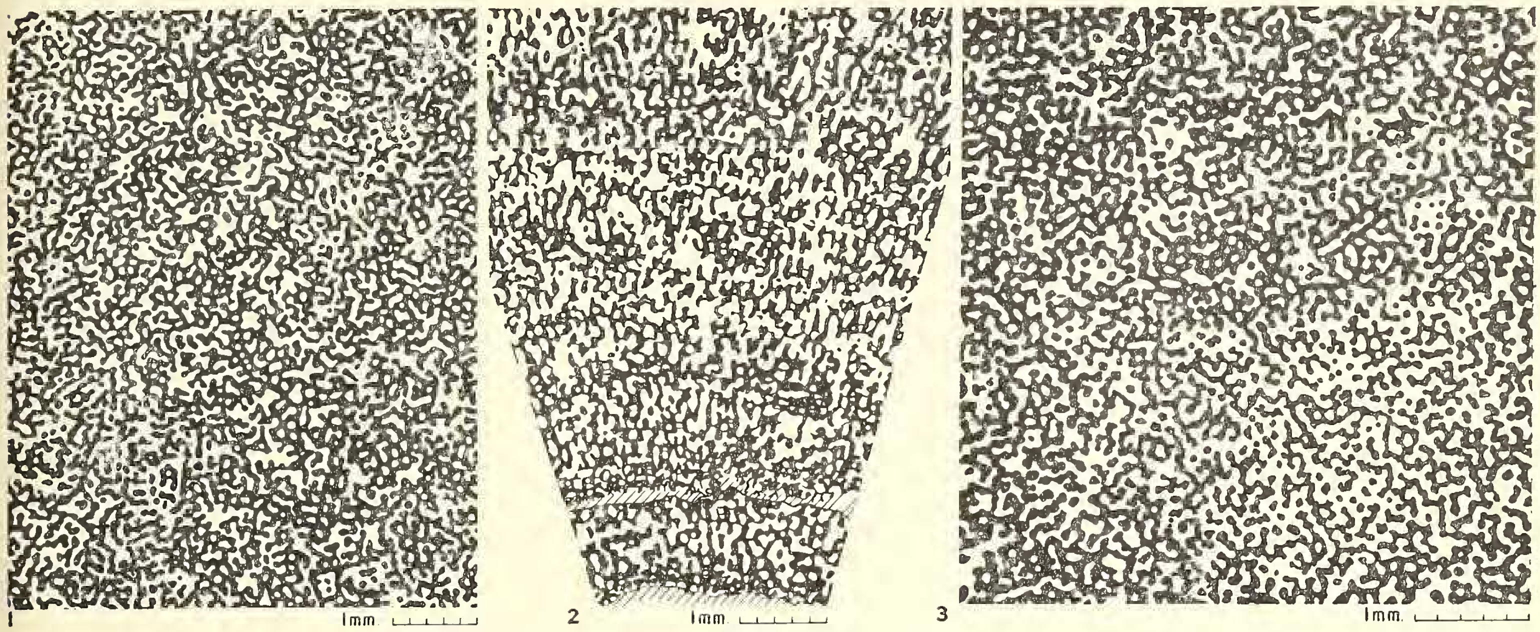
Figs. 2, 3, and 5. *Actostroma nasri* sp. nov. 2, radial section, H 4891b, ×4·1, showing latilamellae of alternate bands of open and compact reticulum. 3, upper right, radial section, remainder oblique or tangential, H 4892a, ×4·1, showing axial and lateral astrotubes in transverse and longitudinal sections. 5, radial section, H 4893b, ×4·1, from holotype, showing latilamellae.



HUDSON, *Actostroma* gen. nov.

a, *b* (text-figs. 1, 2); H 4889, one piece and thin-sections *a*, *b*, *c* (Pl. 15, fig. 4; Pl. 17, figs. 3–5). From the Coral-stromatoporoid beds (Argovian), Kurnub Limestone, Maktesh Hathira, Israel.

Diagnosis. *Actostroma* with slightly latilamellate coenosteum. Reticulum of irregular pillars, mainly continuous, and short transverse bars; transversely vermiculate or tubular, tubules *c*. 0·05–0·07 mm. across, pillars *c*. 0·05–0·07 mm. thick. Transverse bars

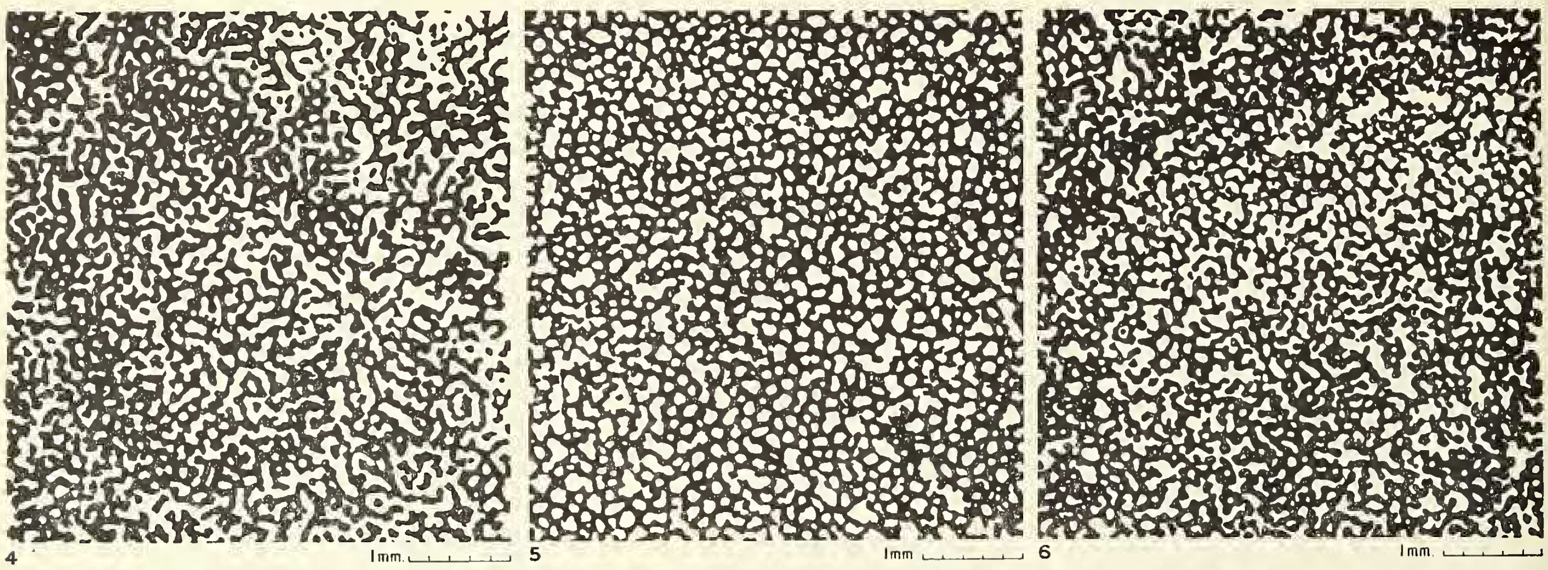


TEXT-FIGS. 1–3. *Actostroma damesini* sp. nov., drawn from photographs of thin-sections. In all three sections the alternating latilamellae are shown by areas of compact and open reticulum. Fig. 1, Tangential section of H 4888b, showing open astrotubes. Fig. 2, Oblique section of H 4888a, showing astrotubes and fine orthogonal reticulum of initial growth, renewed after lime-mud sedimentation (represented by oblique lines). Fig. 3, Tangential section of H 4890b, holotype, showing pillars and pillar-lamellae, astrotubes, and compact and open reticulum.

c. 0·05–0·07 mm. thick, and *c*. 0·07 mm. apart. Astrotubes, *c*. 0·1 mm. across, open to adjacent coenosteal tubules, and hence transversely irregularly stellate, abundant, evenly and well spaced; astrorhizal alignment slight. No astrorhizae.

Description. Coenosteum nodular (largest 4 by 4 by 3 cm.), encrusting, enveloping, mainly corals and stromatoporoids. Surface of fine irregular ostea, with scattered unwalled ostea of astrotubes. No mamelons, no astrorhizae. Coenosteum faintly latilamellate with alternate bands of compact-textured (light-coloured) and open-textured (dark-coloured) reticulum: colour difference due, in part, to difference in proportion of trabecular centres in tissue.

Reticulum of fairly continuous irregular pillars (about 17 in 2 mm.) with, perpendicular to them, discontinuous, very short, transverse connecting processes similar to pillars, forming, in tangential section, a generally tubular mesh in the compact reticulum, and a vermiculate mesh, with many isolated pillars, in the open reticulum. Difference between latilamellae not marked, partly due to thicker pillars and slightly longer transverse bars in compact reticulum. Initial layer of reticulum, about 0·7 mm. thick, finely orthogonal with tubules about half normal width (Pl. 17, figs. 3, 4) and transverse lamellae more continuous. Skeletal tissue almost entirely of trabecular centres, dark, finely mottled and granular, with scattered darker nuclei; outer zone of lighter granular tissue in which grains tend to be elongated or fibrous and generally radially perpendicular (hetergonal). Dark zone of trabecular centres in transverse structures tends to be narrower, less diffuse, and better defined. Tabulae, in astrotubes, transitional in character to transverse structures.



TEXT-FIGS. 4–6. *Actostroma nasri* sp. nov., drawn from photographs of tangential thin-sections. Fig. 4, H 4893a, from holotype, showing traces of astrorhizae within coenosteum, and areas of compact and open reticulum (latilamellae). Fig. 5, H 4892b, compact reticulum showing lateral astrotubes and entire coenosteal tubules. Fig. 6, H 4891a, slightly oblique, showing areas of compact and open reticulum.

Astrotubes, abundant, radial, fairly straight and parallel, unwalled, *c.* 0·1 mm. across, communicating laterally with adjacent coenosteal tubules and thus roughly cruciform, appearing wider in radial section, and difficult to distinguish in tangential section (text-

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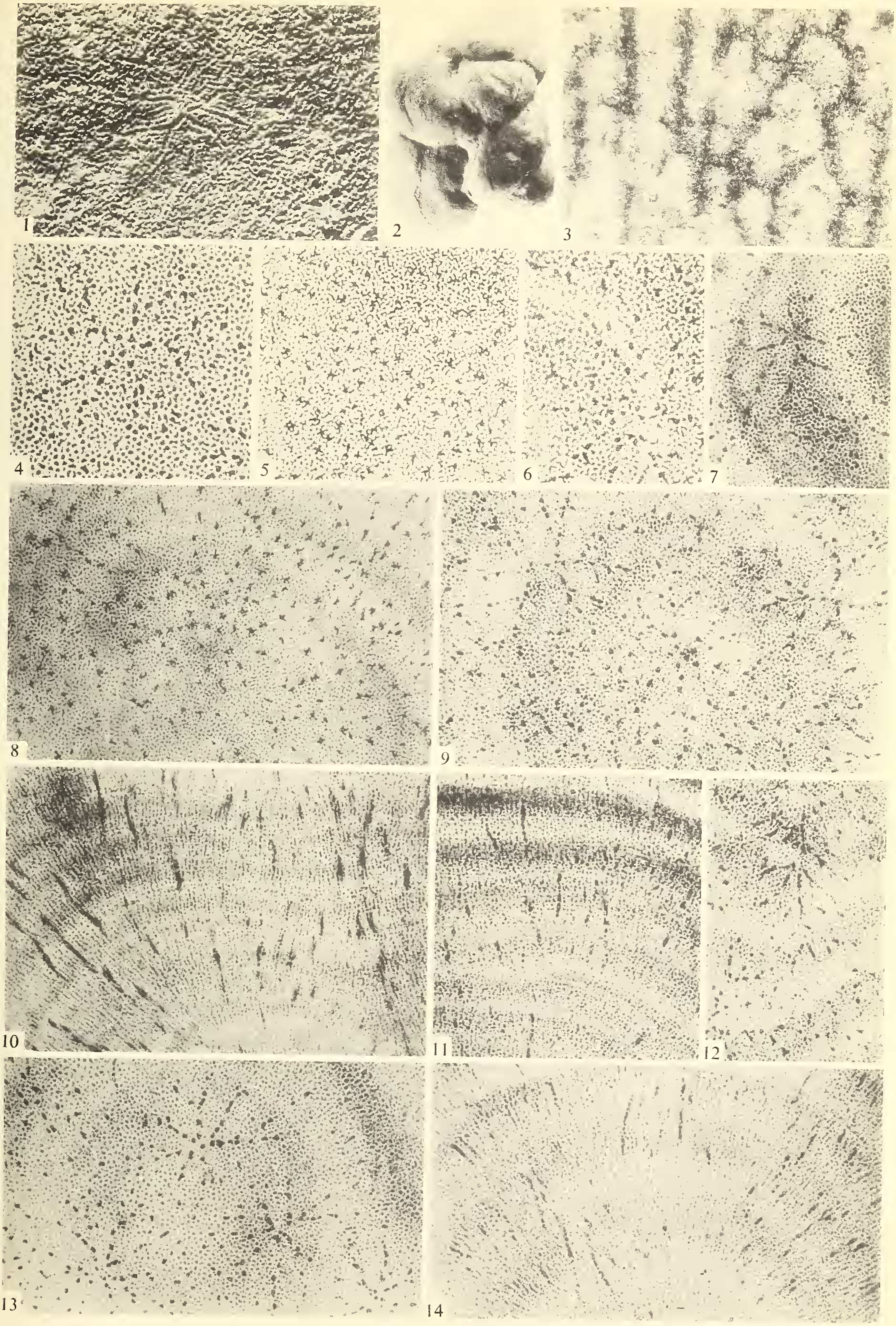
EXPLANATION OF PLATE 16

All specimens from Coral-stromatoporoid beds, Kurnub Limestone (Upper Jurassic), Maktesh Hathira, Israel. Thin-sections (figs. 4–6) and polished surfaces (figs. 7–14), photographed by reflected light and untouched.

Figs. 1, 2, 9. *Actostroma kühni* sp. nov., all of holotype. 1, coenosteal surface, H 4887, ×7, showing astrorhizae connecting ostea of lateral astrotubes. 2, nodular coenosteum, H 4807, ×0·5. 9, tangential surface, H 4887, ×5, showing astrorhizal arrangement of astrotubes.

Figs. 4, 6, 7, 11–14. *Actostroma nasri* sp. nov. 4, tangential section, H 4892b, ×6·5, showing astrorhizal arrangement of astrotubes. 6, tangential section, H 4891a, ×6·5, showing astrotubes and compact and open latilamellae. 7, tangential surface of H 4893/1, ×5, from holotype, showing latilamellae and lateral astrotubes linked by specialized coenosteal tubules. 11, radial surface of H 4893/1, ×5, from holotype, showing latilamellae and astrotubes. 12, oblique surface of H 4891/2, ×5, showing two adjacent systems of astrotubes and connecting coenosteal tubules. 13, tangential surface of H 4892, ×5, showing isolation of astrotubes outside astrorhizal grouping. 14, radial surface of H 4892/1, ×5, showing astrotubes, and coenosteal tubules of astrorhizal radii.

Figs. 3, 5, 8, 10. *Actostroma damesini* sp. nov., all of holotype. 3, thin-section, H 4890a. Photographed, ×52, by transmitted light. Showing heterogonal tissue of vertical and transverse lamellae. 5, tangential section, H 4890b, ×5·75, showing astrotubes joining with adjacent coenosteal tubules. 8, tangential surface, H 4890/1, ×5, showing in centre astrorhizal arrangement of astrotubes. 9, radial surface, H 4890/1, ×5, showing latilamellae and widening of astrotubes due to joining with adjacent coenosteal tubules.



HUDSON, *Actostroma* gen. nov.